Models for Propagating Facilitation in the Insect Visual System

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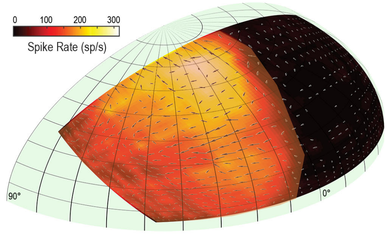
The Phenomenon:

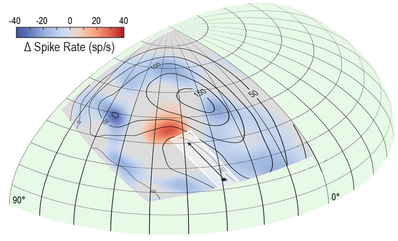
Responsiveness of wide-field ***small target motion detector*** (STMD) neurons in insect lobulae (dragonflies, hoverflies) increased by prior exposure to small targets that move along continuous paths in the visual field.

Characteristics:

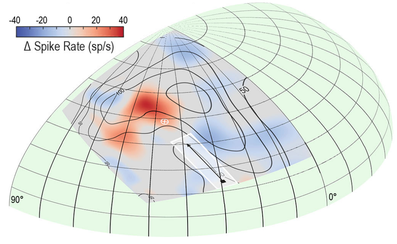
Facilitation appears near/in front of location of moving target (remainder of receptive field *depressed*) => *predictive* function.
Facilitatory 'hot spot' appears to ***propagate*** following cessation of target motion.



Receptive field of STMD neuron CSTMD1 (response to small moving target) in dragonfly



Change in responsiveness induced by small target motion (arrow)



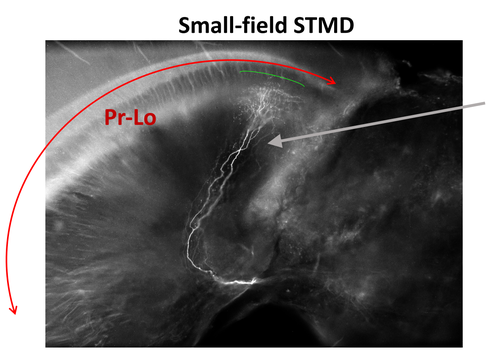
Post-stimulus propagation of facilitation

The Hypothesis:

Facilitation mediated by signal propagation in a ***cellular network***, with activation by & reciprocal interaction with STMDs.

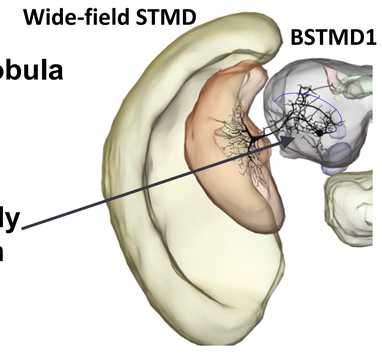
Three Possible Biophysical Mechanisms Investigated:

1. Calcium waves in interconnected glial cells;
2. Calcium waves in neural network;
3. Electrical waves in neural network, retarded by synapses with slow kinetics.

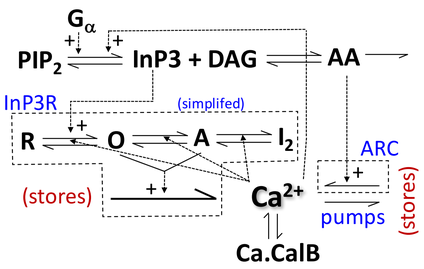
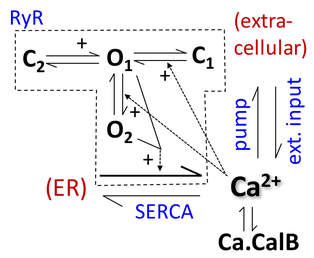
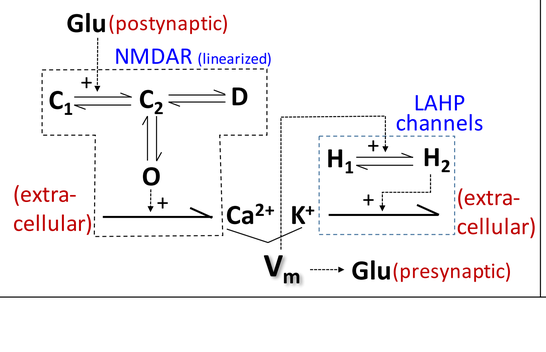


PUTATIVE ANATOMICAL SITES:
***sf*-STMDs arborize / reside in primary lobula (dragonfly)**
- **Receptive field 10°- 15° wide, out of**
- **135° subtense / ~750μm total span**

***wf*-STMDs inputs arborize more centrally**
- **Inputs in deep lobula or central brain**
- **Receptive fields are broad, but**
- **Anatomical spans of dendritic trees proportionally smaller**



Facilitatory network might reside coincident with small-field STMDs in primary lobula, or possibly the dendritic trees of wide-field STMDs. Propagation speed referred to visual field ≅ 40∘/s => 200-250μm/s in primary lobula. (Note: propagation speed in a 1-D cellular process = upper bound for wavefront speed.)

	Model Elements	Transport (leakage not depicted)	Propagation Speed (1-D) (How slow or fast can a wave go?)	Notes
1.	'Astrocytes' w/ 1-D processes InP3 receptors w/ Ca-dependent kinetics (primary Ca channels) InP3 production driven by glutamateric inputs ARC receptors (initial Ca entry) Ca pumps (SERCA & plasma membrane) Ca buffering in cytosol	Rx:  Diff: $\partial/\partial t\,[\mathrm{Ca}^{2+}] = D_{Ca}\,\partial^2/\partial x^2\,[\mathrm{Ca}^{2+}] + J_{Ca}$	< 10μm/s to ~40μm/s Too slow for primary lobula; probably also input regions of wf-STMDs. Speed Limited by receptor kinetics & diffusion of Ca, InP3	Positive feedback: Ca dependence of InP3R's; limited/terminated by InP3R kinetics (distribution among states) & pumps (including nonlinear SERCA).
2.	'Neurons' w/ 1-D processes RyR's w/ Ca-dependent kinetics (primary Ca channels) Ca influx (e.g., through NMDAR's) to initiate waves Explicit ER store of Ca Ca pumps (SERCA & plasma membrane) Ca buffering in cytosol	Rx:  Diff: $\partial/\partial t\,[\mathrm{Ca}^{2+}] = D_{Ca}\,\partial^2/\partial x^2\,[\mathrm{Ca}^{2+}] + J_{Ca}$	~500μm/s (range TBD) Also dependent on Ca diffusion -- why so much faster? Ca-dependent rates in RyR's become so large that as soon as Ca gets from one to the next, it slams wide open.	Positive feedback: Ca dependence of RyR's; limited/terminated by local depletion of ER calcium & nonlinear SERCA pump activation. Induction of Ca entry by external inputs not specified in this model. If from synapses, they would add to the intercellular delay (reduce net speed).
3.	Single-compartment 'neurons' NMDAR's (primary Ca channels) Reciprocal glutamatergic synapses Long after-hyperpolarization (LAHP) following activation		~d/τ_{peak} (d = inter-neuron distance, τ_{peak} = time-to-peak of NMDAR open state impulse response); e.g., 10μm separation ⇔ ~350μm/s. Flexilbe	Positive feedback: Nonlinearity of NMDAR channel current & reciprocal connections between neurons (in network); limited/terminated by LAHP.

Some frames from animated wave in an astrocyte array

Discussion of implications

FINISH CITATIONS!: 1. O'Carroll (1993) *Nature* 362, pp. 541–543; 2. Nordström, O'Carroll (2006) *Proc. Royal Society B*, DOI:10.1098/rspb.2005.3424; 3. Nordström, Bolzon, O'Carroll (2011) *Biology Letters* 7(4), pp. 588–592; 4. Wiederman, Fabian, Dunbier, O'Carroll (2017) *eLife* 2017;6:e26478; 5. Barnett, Nordström, O'Carroll (2007) *Current Biology* 17(7), pp. 569–578.

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